

Status of the southern African *Anapalina* and *Antholyza* (Iridaceae) genera, based solely on characters for bird pollination, and a new species of *Tritoniopsis*

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Anapalina N.E. Br. (1932), erected for several species of long-tubed, red-flowered species previously assigned to *Antholyza* L., is closely allied to *Tritoniopsis* L. Bol. (Lewis 1959a; Goldblatt 1971). Distinctive leaves with more than one main vein (unless very narrow), short coriaceous bracts, the inner longer than the outer, and inflated capsules and large seeds with a loosely to elaborately folded seed coat are synapomorphies uniting the two genera. In addition some species of both genera have unusual pseudopetiolate leaves. Shared, unusually high chromosome numbers, $2n = 32$ and 30 , support the contention that *Anapalina* and *Tritoniopsis* constitute a single monophyletic lineage. The flower of *Anapalina* with its long dimorphic tube, exerted stamens and more or less hooded upper tepal conforms to the classic model for ornithophily and the genus represents no more than a series of species of *Tritoniopsis* adapted primarily for bird pollination. Segregation of genera based solely on this criterion has little merit and such treatment is inconsistent with the circumscription of other genera of subfamily Ixiodeae. The suite of characters associated with ornithophily appears to have evolved several times in Ixiodeae and until recently some natural species assemblages were accorded generic rank on the basis of the adaptations to ornithophily of their flower, while others were placed in genera with other types of floral adaptation. This paper is the second of a series dealing with genera of Ixiodeae defined exclusively by characters associated with ornithophily. Original chromosome counts for the genus and a new species, *Tritoniopsis williamsiana*, are included here. Like *Anapalina*, the genus *Antholyza* [as currently circumscribed *sensu* Brown (1932) and thus excluding the lectotype species] is based on floral adaptations associated with ornithophily. Except for its flowers, it is indistinguishable from *Babiana* Ker-Gawl., in which it was first included by Ker (1804), and then later by Baker (1896). I recommend inclusion of *Antholyza sensu* Brown in *Babiana*, noting their shared plicate leaves, general pubescence or puberulence, and base numbers of $x = 7$. New combinations are provided for the species of *Anapalina* now included in *Tritoniopsis* while the nomenclature of the species until now included in *Antholyza* is outlined.

Anapalina N.E. Br. (1932), geskep vir verskeie spesies wat rooi blomme met lang buise het en wat voorheen aan *Antholyza* L. toegewys is, is naverwant aan *Tritoniopsis* L. Bol. (Lewis 1959; Goldblatt 1971). Kenmerkende eienskappe waardeur die twee genusse verenig word, is blare met meer as een hoofaar (behalwe wanneer baie smal), kort leeragtige skutblare met die binnestes langer as die buitenstes, en opgeblaasde doosvrugte met groot sade waarvan die saadhuif los tot ingewikkelde voue het. Daarbenewens het sommige spesies van albei genusse ongewone blare met skynblaarstele. Gemeenskaplike, buitengewoon hoë chromosoomgetalle, $2n = 32$ en 30 , ondersteun die standpunt dat *Anapalina* en *Tritoniopsis* van monofiletiese oorsprong is. *Anapalina* se blom met sy lang dimorfiese buis, uitgestote meeldrade, en min of meer kapvormige boonste periantblaar, kom ooreen met die klassieke model vir ornitofilie en die genus verteenwoordig bloot 'n reeks *Tritoniopsis*-spesies wat in die eerste plek by voëlbestuiwing aangepas is. Skeiding van genusse wat uitsluitlik op hierdie maatstaf berus, het min waarde en is teenstrydig met die omskrywing van ander genusse van subfamilie Ixiodeae. Die stel kenmerke wat met ornitofilie geassosieer is, het klaarblyklik verskeie kere in die Ixiodeae ontwikkel, en tot onlangs is genusrang op grond van die blom aan sommige natuurlike groepe spesies toegeken, terwyl ander in genusse met ander tipes blomaanpassings geplaas is. Hierdie artikel is die tweede in 'n reeks wat handel oor genusse van die Ixiodeae wat uitsluitlik op grond van kenmerke geassosieer met ornitofilie, omskryf word. Oorspronklike chromosoomtellings vir die genus en 'n nuwe spesie, *Tritoniopsis williamsiana*, word hierby ingesluit. Soos *Anapalina*, is die genus *Antholyza* [soos tans deur Brown (1932) omskryf en daarom met uitsondering van die lektotipespesie] gebaseer op blomaanpassings wat met ornitofilie geassosieer is. Behalwe vir sy blomme, is dit ononderskeibaar van *Babiana* Ker-Gawl., waarby dit eers deur Ker (1804) en later deur Baker (1896) ingesluit is. Ek beveel aan dat *Antholyza sensu* Brown by *Babiana* ingesluit word, en wel op grond van hul gevoude blare, algemene sag- of ylarigheid en basisgetalle van $x = 7$ wat hulle gemeen het. Nuwe kombinasies word voorsien vir die *Anapalina* spesies wat tans in *Tritoniopsis* geplaas is, terwyl die nomenklatuur van die spesies wat tot dusver by *Antholyza* ingesluit is, in breë trekke gegee word.

Keywords: Chromosomes, generic definition, ornithophily, systematics

Introduction

Anapalina was one of nine genera that Brown (1932) recognized, six of them new, for species until then (e.g. Baker 1892, 1896) included in *Antholyza* L. or *Babiana* Ker. At this period *Babiana* included *B. ringens* (L.) Ker, *B. thunbergii*

Ker (syn. *A. plicata* L.f.), very like *B. ringens*, and a number of others of different morphology. Historically *Antholyza* was a genus that included most (but never all) members of Iridaceae that had strongly zygomorphic flowers, nearly all with long-tubed, red flowers. That the criteria used for

recognition of species of *Antholyza* were what we now consider a classical suite of adaptations for bird pollination, has only been properly understood in the last 20 years, although these adaptations were clearly enunciated by Scott Elliot (1890) nearly a century ago.

The criteria for the circumscription of *Antholyza* were never consistently applied. Some species with the *Antholyza*-suite of characters were referred to other genera, e.g. *A. meriana* L. was placed by Miller (1768) in *Watsonia* Mill. and by Thunberg (1784) in *Gladiolus* L. Other species of *Antholyza* were reassigned piecemeal to genera to which various authors considered them allied. Therefore *A. cunonia* L. was referred to a new genus, *Cunonia*, by Miller (1756, 1768) and to *Gladiolus* by Gaertner (1788: 31), in the latter case because of their similar capsules and seeds. *Antholyza ringens* and its close relative, *A. plicata*, were treated as species of *Babiana* by Ker (1804) with which they shared unusual pubescent and plicate leaves and similar *gestalt*. Baker (1896) continued to regard *B. ringens* and *B. thunbergii* as members of *Babiana*, but he maintained *Antholyza* for a number of species, all of which we now consider belong to other genera. Probably for this reason Hitchcock & Green (1929) formally designated *A. cunonia* as the type species of *Antholyza*, a decision endorsed in the code published after the 1930 International Botanical Congress.

Brown's 1932 paper embodied his novel conclusions about the heterogeneous composition of *Antholyza* and *Babiana*, and the genera that Brown recognized were, with minor exceptions, natural i.e. monophyletic and, excepting *Babiana*, holophyletic. However, Brown regarded the typification of *Antholyza* as incorrect and he treated *A. ringens* as the type of the genus. Brown based his opinion on two points: one, that *A. ringens* was the only species known to Linnaeus (1737) when he first described the genus (before 1753); and second, that Linnaeus noted in the protologue of *A. cunonia* (1753) that it might belong to another genus. In *Index Nominorum Genericorum* (Farr *et al.* 1979), *A. ringens* is listed as the lectotype of *Antholyza*, incorrectly as far as I can ascertain, as the original designation of the type by Hitchcock & Green (1929) is still nomenclaturally binding. [I urge that the Hitchcock & Green typification be allowed to stand. The alternative would mean that when *Antholyza* (typified by *A. ringens*) and *Babiana* are regarded as congeneric, the larger *Babiana* is a later synonym, therefore requiring either the transfer of some 62 species of *Babiana* to *Antholyza*, or a formal proposal to conserve *Babiana* against *Antholyza* which seems an unnecessary waste of time and effort, with no assurance of the proposal finding favour].

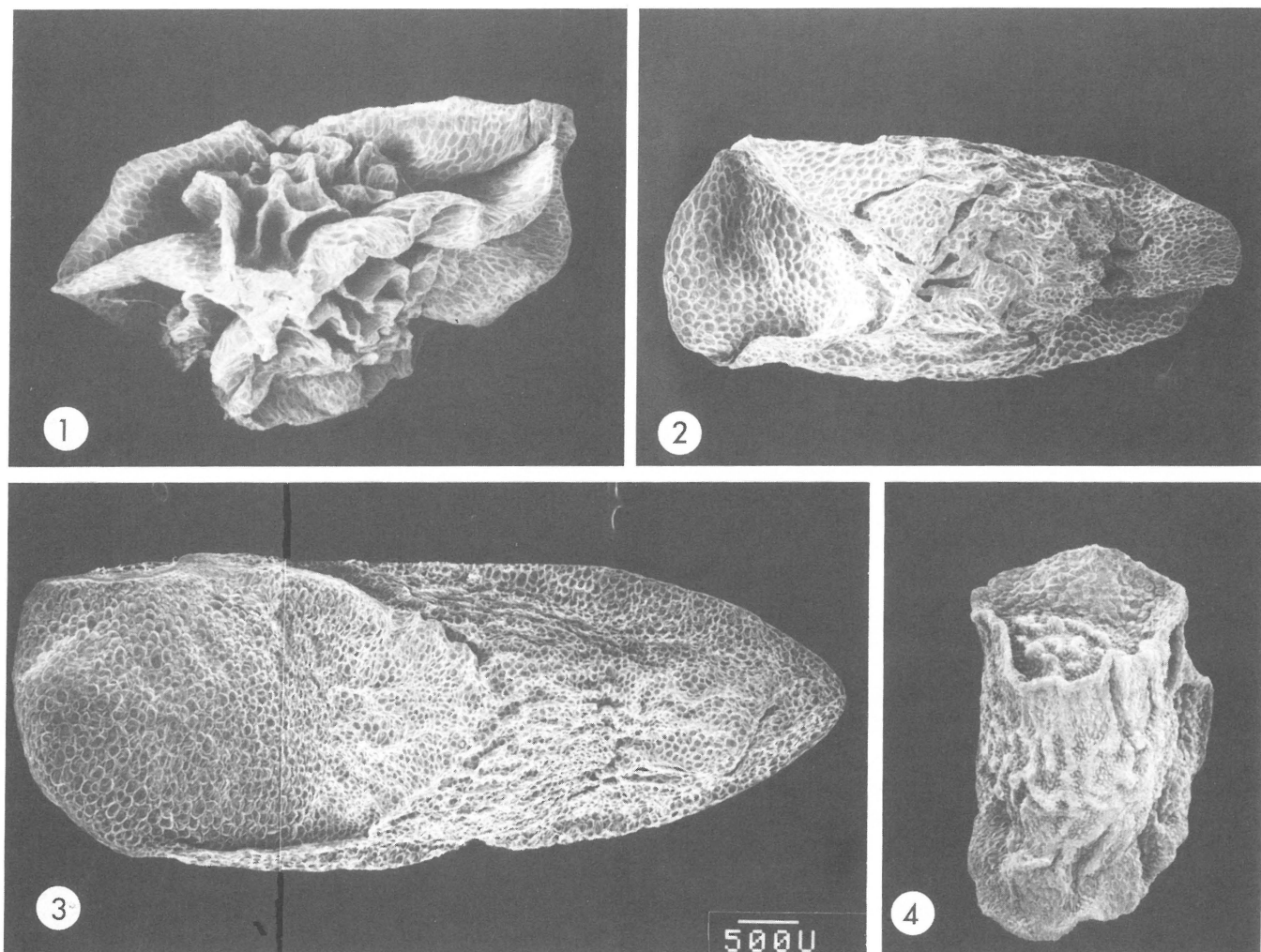
Brown had little to say about the relationships of the genera he recognized at this time. Lewis (1954) tacitly endorsed Brown's treatment and she also demonstrated the diverse affinities of the genera, which she determined using numerous, largely vegetative, characters. Largely on the basis of karyological data (Goldblatt 1971) I supported Lewis's conclusions about the relationships of Brown's genera, but I went further in sinking the monotypic *Curtonus* N.E. Br. (in *Crocasmia* Planch.), the ditypic *Anaclanthe* N.E. Br. (in *Antholyza*) and *Kentrosiphon* N.E. Br. (in *Anomalesia* N.E. Br.). All three were founded on very weak grounds and their affinities were clear.

It was amply clear at this time that an ornithophilous suite of characters had evolved independently in a number of lineages of Iridaceae-Ixiodeae. The taxonomic treatment of the species with these characteristics was, however, never consistent. *Watsonia* remained diverse, including species with flowers that varied from actinomorphic to zygomorphic, and with short, funnel-shaped tubes and either declinate or arcuate stamens or with long dimorphic tubes with a cylindric upper partion. Colours ranged from pink to red and orange. Likewise in *Crocasmia* floral form ranged from actinomorphic to bilabiate with either short funnel-shaped, or long dimorphic tubes. The recognition of genera based exclusively on a suite of floral characters that represent adaptations to ornithophily (or any other pollination syndrome) is unsatisfactory and it is additionally undesirable to have criteria for generic recognition inconsistently applied within a single subfamily. With this in mind Goldblatt & de Vos (1989) proposed the reduction of three genera, recognized as a result of Brown's (1932) work, with the ornithophilous flower type, *Homoglossum* (including *Petamenes*), *Anomalesia* (including *Kentrosiphon*) and *Oenostachys* into *Gladiolus*. Each appears to be allied to a different lineage of the large and diverse *Gladiolus* (ca. 195 spp.) in which ornithophily has probably evolved independently at least four times.

I propose a parallel treatment of *Antholyza* (as currently circumscribed) and *Anapalina*, including the former once again in *Babiana*, and the latter in the closely allied *Tritoniopsis*. The similarities between *Babiana* and *Antholyza* are well established (Ker 1804; Baker 1896; Goldblatt 1971) and need not be discussed here, especially as there is ample precedent for the union of the two genera.

The features which *Anapalina* and *Tritoniopsis* share are less well known, so that it is appropriate to discuss them more fully. Their similarities include: short, at least partly dry, floral bracts; an inner bract entire and longer than the outer; leaves with more than one main vein (unless very narrow); and distinctive large seeds (Figures 1–4) with a reticulate coat extended into large wings or ridges, sometimes with elaborate folds (data partly from Lewis 1959a, 1960). These appear to be the major synapomorphies uniting the two genera. Additionally, at least some of the species of both genera have pseudopetiolate leaves, that is with the basal part considerably narrower than the blade, sometimes very abruptly constricted (Lewis 1954). Shared, unusually high chromosome numbers, $2n = 32$ and 30 , support the contention that *Anapalina* and *Tritoniopsis* are immediately related and monophyletic. The flower of *Anapalina* (e.g. Figure 5) with its long dimorphic tube, the upper part cylindric and ascending to horizontal, the exerted stamens, and typically enlarged and more or less hooded upper tepal conforms to the classic model for ornithophily. There seems little room for doubting that *Anapalina* represents no more than a group of species of *Tritoniopsis* with floral adaptations which are believed to promote bird pollination. Segregation of such species in a separate genus based solely on this set of criteria no longer seems to have merit. Until shown to the contrary, I assume that the species of section *Anapalina* constitute a monophyletic lineage, which is the most parsimonious interpretation in the light of current information.

This paper is the second of a series dealing with genera of



Figures 1–4 SEM micrographs of seeds of *Tritoniopsis*. 1. *T. caffra*. 2. *T. williamsiana*. 3. *T. triticea*. 4. *T. pulchra*. Scale bar = 500 µm.

Ixiodeae defined at least in part, by characters associated with ornithophily. The nomenclature of *Babiana* and *Tritoniopsis* is presented below together with necessary new combinations in *Tritoniopsis* and the protologue for a new species *T. williamsiana*, of section *Anapalina*. Chromosome cytology of *Tritoniopsis* is reviewed together with some original counts for the genus.

Morphology and relationships of *Tritoniopsis*

In her revisions of *Tritoniopsis* and *Anapalina*, Lewis (1959a, 1960) pointed out the several similarities between the genera and she considered them closely related, *Anapalina* differing only in its flower form. The revisions are excellent examples of her consistently good understanding of the biology and systematics of southern African Iridaceae and I do not wish to add to, or change her taxonomy in any way except to make the transfers of species of *Anapalina* to *Tritoniopsis*. Only one novelty has come to my attention, a narrow endemic of marshy sites near Hermanus, at Vogelgat Nature Reserve.

Lewis (1960) enumerated the characters that unite the two genera and it seems worthwhile to briefly repeat them. All may be considered synapomorphies within Ixiodeae.

1. Coriaceous leaves with more than 1 primary vein (unless very narrow);

2. dry brown bracts;

3. the inner bracts (bracteoles) not forked and slightly longer than the outer;

4. corms deep seated, with matted reddish-brown fibers extending upwards in a neck;

5. inflated capsule with large seeds;

6. reticulate seed coat forming wings or ridges and sometimes loosely and elaborately folded in the centre.

These several specialized characters emphasize that *Tritoniopsis* is a well-founded genus but they help little in determining its possible relationships. Leaf anatomical characters are of some value in assessing relationships of Ixiodeae (Rudall & Goldblatt, in press) and I have examined leaves of three species. All have the marginal epidermal cells thickened and columnar, and two, *T. parviflora* and *T. ramosa* have in addition submarginal sclerenchyma, lacking in *T. caffra*. This type of columnar epidermis is uncommon in Ixiodeae, but occurs in *Tritonia* (some species have unspecialized epidermal cells), *Crocasmia*, *Devia*, *Chasmanthe*, *Sparaxis*, *Freesia* and *Anomatheca*, in all of which there is no submarginal sclerenchyma (de Vos 1982; Rudall & Goldblatt, in press). All the above genera, as well as *Tritoniopsis*, are referable to Ixiaceae *sensu* Goldblatt (1990) based on their corm ontogeny. It is likely that the thickened

columnar epidermis is a synapomorphy that unites the above genera (all except *Tritoniopsis*, incidentally have a basic chromosome number of $x = 11$ or 10). Loss of submarginal sclerenchyma is a second synapomorphy for the group (submarginal sclerenchyma is probably basic for Ixiodeae according to Rudall, pers. comm.) excepting *Tritoniopsis*, which also stands out in its apparent paleotetraploid genotype, $x = 16$.

Some other features that may be relevant to the assessment of the affinities of *Tritoniopsis* are as follows: an inflated capsule and seeds with a loose testa (invariably as a circumferential wing) also occurs in *Gladiolus*, which has $x = 15$ and is the only other paleotetraploid genus of Ixiaceae; short floral bracts with the inner not much, or not at all, shorter than the outer also in *Crocasmia*. Until molecular methods are brought to bear on the question of phylogeny of Ixiodeae this question is unlikely to be satisfactorily resolved.

Cytology

Diploid numbers of $2n = 32$ have been recorded for four species of sections *Tritoniopsis* and *Schweiggera* and $2n = 30$ in a fifth. Counts for section *Anapalina* are $2n = 34$ in *T. triticea* and *T. nervosa* and $2n = 32+0-2B$ in *T. caffra* (Goldblatt 1971, 1981). To this list we can now confirm $2n = 32$ in *T. parviflora* (Goldblatt no voucher, from Gansbaai) and report the first counts for *T. flexuosa* (Goldblatt 6114, from Bredasdorp) and *T. williamsiana* (section *Anapalina*) (Goldblatt 8471, from Vogelgat, Hermanus), both $2n = ca. 32$ (or 30) (methodology as described by Goldblatt 1981, 1986). The pattern suggests a base number for the genus of $x = 16$ with descending dysploidy in a species of section *Schweiggera* and possible ascending dysploidy, or supernumeraries in section *Anapalina*. The counts of $2n = 34$ need to be verified.

Systematic treatment

Babiana Ker, Bot. Mag. 16: t. 576 (1802); König & Sims Ann. Bot. 1: 233–234 (1804) (including *Antholyza*). Baker, Fl. Cap. 6: 106–115 (1896) (including *Antholyza*). Lewis, JI S. Afr. Bot. Suppl. vol. 3 (1959b) (excluding *Antholyza*). Type: *B. plicata* (Thunb.) Ker nom. illeg. (= *B. disticha* Ker).

Antholyza sensu Brown, Trans. R. Soc. S. Afr. 20: 265 (1932) excl. the lectotype *A. cunonia* L., Sp. Pl. 37 (1753). Non sensu Ker., König & Sims Ann. Bot. 1: 232–233 (1804) et Baker, Fl. Cap. 6: 165–171 (1896).

1. Babiana ringens (L.) Ker, König & Sims Ann. Bot. 1: 233 (1804). Baker, Fl. Cap. 6: 114 (1896).

Antholyza ringens L., Sp. Pl. 37 (1753).

2. Babiana thunbergii Ker, König & Sims Ann. Bot. 1: 233 (1804). Baker, Fl. Cap. 6: 114 (1896).

Antholyza plicata L.f., Suppl. Pl. 37 (1782) [existence of *Babiana plicata* Ker bars transfer of *A. plicata* L.f. to *Babiana*].

Anaclanthe plicata (L.f.) N.E. Br., Trans. R. Soc. S. Afr. 20: 269 (1932).

Anaclanthe namaquensis N.E. Br., Trans. R. Soc. S. Afr. 20: 269 (1932).

Tritoniopsis L. Bolus, S. African Gard. 19: 123 (1929). Lewis, JI S. Afr. Bot. 23: 319–355 (1959a) (including full generic synonymy). Type: *T. leslei* L. Bolus.

Section 1. Tritoniopsis (one species).

Section 2. Schweiggera (E. Mey. ex Baker) G. Lewis, JI S. Afr. Bot. 23: 323 (1959b) (13 species).

Section 3. Anapalina (N.E. Br.) Goldbl. comb. & stat. nov.

Anapalina N.E. Br., Trans. R. Soc. S. Afr. 20: 274 (1932). Lewis, JI S. Afr. Bot. 24: 51–72 (1960) (8 species). Type: *A. triticea* (Burm.f.) N.E. Br. [= *T. triticea* (Burm.f.) Goldbl.] (See Lewis, 1960 for the species descriptions and more extensive synonymies of all except the new *T. williamsiana*).

1. Tritoniopsis triticea (Burm.f.) Goldbl. comb. nov.

Ixia triticea Burm.f., Flora Cap. Prod. 1 (1768).

2. Tritoniopsis burchellii (Burm.f.) Goldbl. comb. nov.

Antholyza burchellii N.E. Br., Kew Bull. 1929: 136 (1929).

3. Tritoniopsis pulchra (Baker) Goldbl. comb. nov.

Antholyza pulchrum Baker, Fl. Cap. 6: 531 (1896).

4. Tritoniopsis longituba (Fourc.) Goldbl. comb. nov.

Anapalina longituba Fourc., Trans. R. Soc. S. Afr. 21: 76 (1932).

5. Tritoniopsis nervosa (Thunb.) Goldbl., comb. nov.

Antholyza nervosa Thunb., Prodr. 7 (1794).

6. Tritoniopsis intermedia (Baker) Goldbl. comb. nov.

Antholyza intermedia Baker, Handbk. Irid. 230 (1892)

7. Tritoniopsis caffra (Ker ex Baker) Goldbl., comb. nov.

Antholyza caffra Ker ex Baker, Handbk. Irid. 230 (1892).

8. Tritoniopsis williamsiana Goldbl. sp. nov.

Type: South Africa. Cape: Vogelgat Nature Reserve near Hermanus, mountain marsh after fire, ca. 425 m, Goldblatt 8471 (holotype, NBG, isotypes, K, MO, PRE). Figure 5.

Plantae 40–80 cm alta raro ramosae, cormo 12–18 mm diam., tunicis mollibus fibrosis, spica 12–18 florum, bracteis exterioribus 14–15 mm, interioribus 16–18 mm longis, floribus rubris zygomorphis, tubo perianthii dimorpho, infra ca. 12 mm longo erecto, supra ca. 12 mm longo 4.5 mm diam., tepalis inaequalibus, superiore longiore ca. 20 mm longo, antheris ca. 6 mm longis purpureis apiculatis, capsulo ellipsoideo 7–9 mm longo, seminibus bialatis, ca. 5 mm longis.

Plants usually solitary, 40–80 cm high. *Corm* globose-depressed, 12–18 mm diam., tunics soft-textured, finely fibrous, not forming a neck. *Leaves* about 6, the lower 3–4 basal, 15–25(–30) cm long and less than half as long as the



Figure 5 Habit and flowers of *Tritoniopsis williamsiana*. Habit $\times 0.5$, separate flower, half flower and bracts, full size. (Del. M.L. Branch.).

stem, narrowly lanceolate, narrow below but without a distinct petiole-like base, firm-textured, 5–7 mm wide, 2–3 nerved, the upper 2–3 leaves cauline, reduced in size, the uppermost becoming bract-like. Stem erect, 3–4 mm diam., rarely with a branch. Spike 12–18 flowered, the flowers spirally arranged, bracts dark red-brown, broadly lanceolate, dry in the upper half at anthesis, outer 14–15 mm long, inner 16–18 mm long. Flowers zygomorphic, scarlet, the lower three tepals with a darker median vein; perianth tube dimorphic, slender, erect and cylindric below, curved at the knee and widely cylindric and ascending above, lower part ca. 12 mm long, upper part ca. 12 mm long, 4.5 mm in diam.; tepals unequal, the uppermost to 20 mm long, ca. 6 mm wide in the upper third, horizontal and hooded over the anthers, ultimately curving upwards distally, upper laterals ascending and recurving distally, ca. 15 mm long, dry apically, the lower tepals recurved, to 18 mm long, spatulate, to 5.5 mm

wide in the upper third, margins undulate, upper three tepals joined for 2 mm more than the lower. Filaments inserted at base of the upper part of the tube, ca. 28 mm long, submedianly fixed, unilateral, arched below the upper tepal; anthers ca. 6 mm long, dark purple, with red apiculus 1 mm long. Ovary ca. 3 mm long, style arching above the filaments, branches dividing near the anther apices, curving downward and the branches unfolding when pollen shed, branches ca. 2 mm long, expanded apically. Capsule broadly ellipsoid, 7–9 mm long, rugose, reddish to maroon; seeds ca. 5 mm long, 2–3 mm wide, red-brown, reticulate, the coat forming a wing at the distal and proximal ends. Chromosome number $2n = 32(-30)$.

Flowering time: mid January to mid February.

Distribution

Tritoniopsis williamsiana has been recorded only in Vogelgat Nature Reserve in the Klein River mts. near Hermanus in the Caledon district. It apparently blooms only after fires, hence its discovery in January 1987, after a fire in February the previous year. The species is restricted to somewhat marshy, seepage zones at an elevation of ca. 425 m. The habitat supports a dense, tall growth of *Berzelia* (Bruniaceae) and close ground cover of Restionaceae and Cyperaceae, which in the second year after a fire, form a dense growth that shade out *T. williamsiana*.

The flower has the classic suite of characters for bird pollination and I noted visits by orange-breasted sunbirds which probe the flower, presumably foraging for the nectar produced in the lower part of the tube. In doing so the pollen is probably deposited on the head of the bird and transferred to the receptive stigmas of flowers visited subsequently.

Diagnosis and relationships

The red flowers of *Tritoniopsis williamsiana* have a long dimorphic perianth tube with a cylindric upper part and unequal, spatulate tepals, the uppermost of which is largest and initially hooded over the stamens. In these features it resembles section *Anapalina*, notably *T. longituba*, *T. nervosa* and *T. caffra* more closely than those of the section that have nearly equal tepals. Distinctive features of the flower are the red anthers and dark red median markings of the lower tepals. *Tritoniopsis longituba* has similar tepal markings but yellow anthers, and it has a larger flower with a tube 28–40 mm long (Lewis 1960) as compared with ca. 24 mm in *A. williamsiana*. In its vegetative morphology *A. williamsiana* differs from other species of section *Anapalina* in its relatively soft-textured leaves, the 2–3 main veins of which are not as prominent as in other species. Also, the base of the leaves forms a poorly defined petiole. The corms are relatively small, to 15 mm in diam. and the tunics are soft-textured and do not form a neck such as is present in all other species of *Tritoniopsis*. The flattened 2-winged seeds are also distinctive, as other members of the section have 3–4 sided and angled seeds. The soft-textured tunics and small corms may be correlated with the wet habitat which is unlike the dry open situations favored by other species of *Tritoniopsis*. *Tritoniopsis williamsiana* does not seem to be especially close to any of the other species of section *Anapalina*,

although in Lewis' (1960) key it comes closest to the SE Cape *T. intermedia*.

Specimens examined

—3419 (Caledon): Vogelgat, Hakealand and towards Sip, black peaty almost marshy soil, 400–440 m (–AD), 24 Jan. 1987, Williams 3776 (HER-V, MO, NBG); Vogelgat, above Main Stream, 400–440 m, 21 Mar. 1987 (fr.), 3791 (HER-V, K, MO, NBG); Vogelgat Nature Reserve near Hermanus, mountain marsh after fire, ca. 425 m, 30 Jan., 1987, Goldblatt 8471 (BOL, K, MO, NBG, PRE, WAG).

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